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## On the Status of the Family Desmognathidae (Amphibia, Caudata)

BY

E. IVÁN SOLER,

Mayaguez, Puerto Rico

ABSTRACT: The anatomical features of the salamanders of the genera *Desmognathus* and *Lewognathus* are re-examined. Especial study of the characteristics of the vertebrae is made. The author concludes that the vertebrae differ basically from those of the family Plethodontidae and that this fact, together with numerous other anatomical differences, warrants the re-establishment of the family Desmognathidae. He includes the genera *Lewognathus* and *Desmognathus*.

### INTRODUCTION

The genus *Desmognathus* comprises a group of common North American salamanders, which occur from the southern extreme of New Brunswick southward to northern Florida and southwestward to the eastern extremes of Texas and Oklahoma. There are at present eleven species and subspecies recognized in this genus. The anatomy, physiology, and life history of the animals of this group have been extensively investigated and are well known. The ready availability of these animals where they occur makes them ideal for such investigations. Mrs. I. W. Wilder (1913) published a complete work on the life history of *Desmognathus fuscus*. Seelye (1906) investigated the circulatory and respiratory systems of this species. Fish (1895) published a detailed account of the nervous system and its development in the same species. Other authors also have reported upon their investigations of this and other forms of *Desmognathus*. The ecology of the various species of this genus has also been detailed at various times chiefly by G. K. Noble, E.

R. Dunn, C. H. Pope, and C. S. Brimley. A considerable literature has appeared on the taxonomy of the salamanders of the genus *Desmognathus*.

In contrast to the general agreement among workers upon the anatomy, physiology, and life histories of the members of this genus, the taxonomic literature indicates a marked disagreement as to the higher taxonomic categories. Baird (1849) used this name to denote a genus that then contained only the three known species: *D. fuscus* (Rafinesque), *D. auriculatus* (Holbrook) [= *D. fuscus auriculatus*], and *D. niger* (Green) [= *D. quadramaculatus quadramaculatus*]. In 1866, Cope proposed the family Desmognathidae, with the single genus *Desmognathus*, and in 1869, he published a complete classification of the lungless salamanders proposing another family Thoriidae having a single type genus *Thorius*.

Boulenger in 1882 placed the then recognized families Salamandridae, Amblystomatidae, Plethodontidae, and Desmognathidae together in a single family Salamandridae. He arranged each of the former families as subfamilies and placed the genus *Thorius* in the subfamily Desmognathinae.

Cope again in 1889, in his "Batrachia of North America" persists in maintaining family rank for the Desmognathids and the other groups that Boulenger had reduced to subfamily status. Thus a *status quo* was reached, with zoologists adhering either to Boulenger's or Cope's classification.

In 1892 Stejneger described a new genus *Typhlotriton* ascribing it to the family Desmognathidae following Cope's classification. In 1893 Cope described a new genus *Haptoglossa* from Costa Rica and revised his concept of the thoriid group reducing it to subfamily rank as Thoriinae under the Desmognathidae and referring to it three genera: *Thorius* Cope, *Typhlotriton* Stejneger, and *Haptoglossa* Cope. Moore in 1899 described *Leurognathus*, a new genus of the family Desmognathidae.

In 1900 Moore, basing his opinion on his own observations and those of Vaillant in 1882 and 1886, concluded that the family Desmognathidae was not valid. He based his conclusions solely on the characteristics of the articulation of the vertebrae. He included the desmognathid group in the family Plethodontidae, yet did not exclude the possibility of its classification as a subfamily.

Fowler in 1907 and Hurter and Strecker in 1909 retained the Desmognathidae as a valid family. In 1908 Brown designated *D. fuscus fuscus* (Rafinesque) as the type species of the genus *Desmognathus*

and also retained the family Desmognathidae. In Mrs. Wilder's work "The life history of *Desmognathus fuscus*" in 1913, she considered the genus *Desmognathus* to be a member of the family Desmognathidae. However, in 1912 Brimley placed *Desmognathus* as a genus of the family Plethodontidae, as did Fowler and Dunn in 1917. Nevertheless Dunn in the same year treated the genera *Desmognathus* and *Leurognathus* as members of the plethodontid subfamily Dismognathinae (*sic*).

In 1917 Stejneger and Barbour considered *Desmognathus* under the family Plethodontidae. Finally in 1926 Dunn placed *Desmognathus* under the Plethodontidae, but did not mention his previous subfamily Dismognathinae. Although he suggested some form of generic grouping of the plethodonts, he made no attempt at actual taxonomic differentiation of these generic groups. From 1926 until the present, Dunn's classification has been generally used. However, Taylor (1944: 193 and 204) questioned Moore's reasons for invalidating the Desmognathidae. Very recently Smith and Taylor (1948) have come to recognize the Desmognathidae as a valid family.

Since it has been shown that there are still uncertainties and differences of opinion as to the higher taxonomic categories of this group, it has become apparent that a re-examination of the problem is absolutely necessary. Consequently I have re-examined such material as is listed below and I have noted similarities and differences among these groups, especially as regards the Plethodontidae. I have tried to weigh carefully their relative importance, and on this basis award this group of salamanders the taxonomic rank which it seems to deserve. The following points are considered:

1. That the principle of taxonomic differentiation on the basis of vertebral articulations in salamanders is still a concept that must be applied to differentiate between the Desmognathidae and other families.

2. That the family has other differentiating characters besides the vertebral articulations—characters which must be taken into consideration in evaluating the taxonomic rank and relations of this group.

3. That the Desmognathidae is a valid family.

4. That the family Desmognathidae comprises the two genera *Desmognathus* and *Leurognathus*. The possibility of a third genus, *Haptoglossa*, is considered.

## MATERIALS AND METHODS

There have been available for study specimens and skeletons of *Desmognathus fuscus fuscus*, *D. fuscus brimleyorum*, *D. fuscus auriculatus*, *D. ochrophaeus ochrophaeus*, *D. ochrophaeus carolinensis*, *D. quadramaculatus quadramaculatus*, *Leurognathus marmorata marmorata*, and *L. marmorata intermedia*. I have studied material of the following plethodontid genera: *Plethodon*, *Thorius*, *Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Ensantina*, *Chiropterotriton*, *Hydromantes*, *Batrachoseps*, *Hemidactylium*, *Manculus*, *Pseudoeurycea*, *Magnadigita*, and *Bolitoglossa*. I have also studied family characteristics as evidenced by skeletal and preserved material of *Taricha*, *Diemictylus*, *Siren*, *Necturus*, and *Ambystoma*.

The procedure followed was first, to make examination of osteological material of the various species of *Desmognathus* and *Leurognathus*. Then comparisons were made with skeletal structures of the genera previously mentioned. Emphasis was placed on the morphology of the vertebral column and cranial structures although other characters were also observed. Secondly, a comparative study of the musculature of various species of *Desmognathus* and *Leurognathus* were undertaken and again comparisons were made with the other forms. Emphasis here was given chiefly to the muscles of the head and throat.

Owing to limited time a study of the microscopic anatomy of these forms was not feasible. However realizing the possibility that important taxonomic characters might be found in these structures, I have endeavored to examine the more pertinent literature dealing with the various systems and organs. From this source a considerable number of characters have been discerned which have direct bearing on the problem.

## ACKNOWLEDGMENTS

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## VERTEBRAL DIFFERENCES

Boulenger (1882: 2) and Cope (1889: 33) separated the Desmognathidae from the Plethodontidae chiefly on the basis of their vertebral articulation. The desmognathids were regarded as having opisthocoelous vertebrae while the plethodonts were considered as being amphicoelous. Moore (1890: 621) considered the vertebral articulation as the only character of significance that created distinction between these two families. He claimed that the condition of the vertebrae is dependent on the age of individual animals, and consequently of no value as a systematic character for the separation of families. While *Hemidactylum*, *Plethodon*, and *Ancides* never become opisthocoelous, he stated that *Pseudotriton ruber* and *Gyrinophilus porphyriticus* show a progressive ossification of the intervertebral cartilage throughout life until old adult specimens reach an opisthocoelous condition; and that a condition comparable to *Desmognathus* is reached in *P. ruber* at 180 mm. and in *G. porphyriticus* at 200 mm. in length. I have not been able to obtain specimens for investigation with these exact measurements. In fact the largest specimen of *P. ruber* examined by Bishop (1946) was only 178 mm., two mm. short of that which Moore estimates as the probable length of his specimen. The largest specimen of *P. ruber* in the Museum of Natural History of the University of Kansas measures only 155 mm. I have procured through the kindness of Doctor Bishop a specimen of *G. porphyriticus* 190 mm. long, which approaches very closely the size of the specimen used by Doctor Moore. I dissected both specimens and I found what might be called a "false" opisthocoelous condition. Immediately after dissection the anterior vertebral articulation exhibits a bulbous condyle in both species, yet by simply touching or probing this structure one finds out that it is soft and not ossified. This fact is further confirmed when the vertebra is dried out and this knob shrinks back into the cup.

However, in *Desmognathus* and *Leurognathus* a true opisthocoelous condition is achieved at an early age. I have dissected a specimen of *D. ochrophaeus ochrophaeus* of only 55 mm. and one of *D. fuscus fuscus* 60 mm. in length in which already the process of ossification had extended beyond the border of the cup. Thus the morphological results of this process of ossification are present in *Desmognathus* throughout approximately the whole life of the animal. In such genera of plethodonts where this process is said to occur, its results are present only in the very old adult stages.

Sagittal sections of the vertebrae of *Desmognathus*, *Thorius*, *Gyrinophilus* (140 mm.), *Pseudotriton* (135 mm.), *Pseudoeurycea*, *Plethodon*, and *Taricha* were made. To accomplish this the vertebrae were imbedded in transparent plastic blocks and then the surface was reduced to the desired level with fine sandpaper. The results have been decisive in demonstrating the clear cut differences in the vertebral articulations existing between the desmognathids and other genera of urodeles. The anterior part of the centrum of *Desmognathus*, as shown in Pl. X, fig. C, is a solid bony structure filling the cup and appearing homogeneous with the walls of the centrum leaving no trace of any part of a notochordal canal in the anterior half of the centrum of the vertebra. A solid condyle protrudes anteriorly. The posterior part is typically hollow. Thus the vertebrae are typically amphicoelous. *Thorius* and *Taricha* are externally opisthocoelous with a well-defined condyle. However, this is somewhat misleading since the anterior articulating condyle is merely a convex ossified cap fitting over the anterior opening of the cup, while the cup itself is hollow (see Pl. X, figs. A and B).

The notochordal canal of the centra of *Gyrinophilus* and *Pseudotriton* show notochordal cartilage, but no bone. Thus for all practical purposes they are still amphicoelous forms like *Plethodon*. (See Pl. X, figs. D and E). The cartilage present in the vertebrae occupies only the anterior edge of the cup, leaving a hollow cavity behind it. In still older forms this cartilage protrudes anteriorly in the form of a condyle in which there may be some deposition of calcium. However, this shrinks back upon drying, or if allowed to macerate will disappear completely. In the *G. porphyriticus* (190 mm. long), it was found that the posterior portion of the notochordal cartilage had become calcified or ossified, however, not filling the posterior part of the cup. This calcified portion did not extend forward to the edge of the cup and furthermore, unlike *Desmognathus*, it was easily distinguishable from the bony walls of the centrum. The condylar portion of the intervertebral cartilaginous mass still remained soft and shrank upon exposure.

The term, opisthocoelous, still describes externally the vertebrae of *Desmognathus*, *Leurognathus*, *Taricha*, and *Thorius*; and the term amphicoelous is likewise applicable to all plethodonts except *Thorius*. However, to differentiate between these forms the classification of vertebrae now needs something more than terms descriptive of external appearance. A sagittal section shows three very distinct internal conditions of the vertebral centrum. To describe these I propose the following terms:



The term "holocoelous," meaning entirely hollow, is proposed for that type of vertebral centrum typical of many plethodonts and various other primitive salamanders. This term is descriptive of the notochordal canal when there is no evidence of calcification or ossification of the material enclosed therein.

For the condition of the vertebral centrum in *Desmognathus* and *Leurognathus* the term "hemicoelous" or half hollow, is proposed. This term is descriptive of that condition in which the posterior half of the notochordal canal is hollow and the anterior half is solid bone including a condyle projecting from it.

"Pseudocoelous" is proposed to describe that condition of the notochordal canal such as obtains in *Thorius* and *Taricha*. Here the canal itself is hollow, yet it is covered at its anterior end by an ossified cap which, when observed from the outside, conveys a false impression of having a condition similar to that found in *Desmognathus*. It is also a term applicable to very old adult specimens of *Gyrinophilus* and *Pseudotriton* where there may be calcification within the centrum of a part of the notochordal cartilage.

But the condition of the vertebral articulation and the characteristics found in the centrum are not the only differences between the genera of Desmognathidae and the genera of Plethodontidae. Upon close examination of the vertebral column one finds further characteristics that thus far have only been suggested (Dunn 1926, and others), but not used in the differential taxonomy of the group. Dunn points out that the atlas of *Desmognathus* and *Leurognathus* is very different from that found in plethodonts. There is a gradual curving upward of the dorsal part of the arch of the atlas which forms a sharp-angled elevation where it meets the vertically arranged supraposterior surface (see Pl. XI, fig. B and C). This strong, sharp-edged, wide elevation serves as a posterior point of attachment for the tendon that immobilizes the temporalis muscle. This surface formed by the elevation also serves as an anterior point of attachment for the ends of some fibers of the dorsal longitudinal muscles. The atlas of plethodonts has a plane horizontal dorsal surface and there is no vertically arranged supraposterior surface as such. No doubt this elevation in *Desmognathus* and *Leurognathus* has been caused by the pulling stress of the temporal tendon upon the dorsoposterior angle of the atlas throughout the evolution of the forms.

The lateral articulating facets of the odontoid processes of the atlas of most, if not all, plethodonts are fused medially by a thin

sheet of bone. In *Desmognathus* and *Leurognathus* this ossification has not taken place and the two facets are distinctly separated and very much reduced, practically nonexistent.

The remainder of the vertebral column of *Desmognathus* and *Leurognathus* exhibits characteristics typical of most urodele vertebrae. However, there are pointed processes arising from the dorsal surfaces of the postzygapophyses of the anterior presacral vertebra which do not occur in plethodonts (see Pl. XI, figs. D and E). In younger specimens these processes are normally present only in the first three or four presacral vertebrae, excepting the atlas, but in older specimens these appear present to the tenth or thirteenth vertebra. I have not observed them present posterior to the thirteenth vertebra.

### CRANIAL CHARACTERS

In studying the skull of *Desmognathus* and *Leurognathus*, I have followed an anteroposterior sequence. The skulls of these forms are relatively large, yet keeping a size which is related to the general proportions of the body. They are completely ossified units with firm sutures. The anteroposterior streamlining of the skull gives testimony to the aquatic evolution of the group. The widening of the external surface of the spines of the premaxilla is especially eloquent in this respect. In the characters of the premaxilla we find the main generic difference between *Desmognathus* and *Leurognathus*. The latter has no premaxillary fontanelle, while the former has a rather large one. Nevertheless both genera have the paired premaxillary foramina. The wedge shape of the snout in both forms must be the resultant of the underwater "rooting" habits of these forms.

The frontal bone that joins directly with the maxilla owing to the absence of a prefrontal, has a ventrolaterally directed process which arises from the side of the frontal bone, borders the anterior part of the orbit, and forms an osseous division between the nasal chambers and the orbits of the eyes. The origin of this process is open to speculation. It definitely is not present in the related families Plethodontidae and Salamandridae.

The parietals have been subjected to great stress by the temporalis muscle and its contained tendon. This muscle runs along the dorsal surface of the parietal where the latter forms a suture with the periotic. It then turns ventrally on the anterior edge of the parietal to insert on the coronoid process of the mandible. A rounded groove in which the muscle lies, is present on the dorsal surface of the bone



and, furthermore, the portion of the parietal bordering the orbit has been extended somewhat forward, thus considerably reducing the length of the orbit. In most plethodonts the length of the orbit is approximately one half or more of the total length of the skull. However, in *Desmognathus*, owing to the condition of the parietals, the length of the orbit is about one third of the total cranial length.

Another striking difference between the Desmognathidae and the Plethodontidae is the morphology of the occipital condyles. In the plethodonts which I have examined the condyles are sessile and their articulating surface are either plane or concave. In *Desmognathus* and *Leurognathus* there are two stalked condyles measuring one or two millimeters in length, extending posteriorly from the skull, and with a convex surface to articulate with the concave facets of the atlas.

The morphology of the mandible provides a constant difference which is undoubtedly of taxonomic value. The coronoid bone of most plethodonts forms a low, gently tapering, elliptical curvature on the posterodorsal edge of the mandible. But in *Desmognathus* and *Leurognathus* the temporalis and its stress on the adjacent bones have produced a change from this form, and the coronoid process formed in these genera is an acute, pyramidal elevation of the posterodorsal edge of the mandible. Its upper tip is the point of insertion of the temporalis. One may readily infer that this, just as the already described peculiar formation of the atlas and the grooving of the parietal area of the skull, is a result of the stresses of the temporal tendon. This also shows one example in amphibians of what Gregory (1933: 446) has so painstakingly shown in fishes when he says: "The facts cited in this paper sufficiently prove that in the skull of the fish, just as in the mammalian skeleton, bony trabeculae, ridges, buttresses, etc., arise in response to specific stresses, such as those generated by the thrusts of one moving part upon another, in other words, that bones are usually strengthened in proportion to the loads they bear."

#### DENTITION

Relatively little work has been done on the dentition of salamanders in general. The teeth of salamanders are usually very small and in live and preserved specimens they are partially concealed under a layer of epithelium. Nevertheless, in skeletons the dentition may be easily studied under a low power microscope. Desmognathids and plethodonts usually have pleurodont teeth arranged along the buccal ridges of the maxilla, premaxilla, and mandible.

However there is a considerable variation among plethodonts as to the maxillary teeth. While *Thorius* has an edentulous maxilla,\* *Batrachoseps* has various rows of teeth along the maxilla. Both families also have vomerine and paravomerine† patches of teeth. These may be arranged in either continuous or discontinuous patches. Male desmognathids tend to lose the vomerine teeth, this effect being more accentuated in some species than in others. This tendency to lose completely the vomerine teeth is not found in plethodonts.

Noble in 1927 and Noble and Pope in 1929 linked dentition in *Desmognathus* to secondary sexual characteristics. Secondary sexual dimorphism is evident in many other urodele genera, but its effects in desmognathids are unique and quite different from those found in other forms. The tendency to complete loss of the vomerine teeth seems to be restricted to desmognathids alone. Other secondary sexual characteristics like the elongation and forward protrusion of the premaxillary teeth and the tendency to lose the posterior maxillary teeth are mutually shared with some genera of plethodonts and perhaps other families.

#### THE HYOBRANCHIAL APPARATUS

One of the most significant differences between the Desmognathidae and the Plethodontidae is found in the hyobranchial apparatus of the larvae of *Desmognathus* and *Leurognathus*. Mrs. Wilder (1913: 300) had already noticed in her study of the life history of *Desmognathus* the presence of four gill slits in the larvae of these forms. But this condition did not seem extraordinary to her as she correctly considered the genus to belong to the family Desmognathidae. This is a radical departure from the typical condition in the larvae of the Plethodontidae which have only three gill slits. However, more recently, Hilton (1947: 191), after examining the hyoid apparatus, comments as follows: "In all the genera of Plethodontidae examined, two only have four pairs of branchial arches, *Desmognathus* and *Leurognathus*. This may show that these are closely related and also suggest that they are more definitely related to other groups than the rest of the family so far known, for they all have the rather distinctive number of three pairs of branchial arches."

The adult hyobranchial skeleton of *Desmognathus* has been studied by Piatt in 1935 and compared with that of various genera

\* Cope in his "Batrachia of North America," Pl. 37, figs. 2-4, shows a skull labeled as *Thorius pennatulus*, having maxillary teeth. This is obviously an error, as all the known species of *Thorius*, including *T. pennatulus*, have an edentulous maxilla.

† I follow Taylor (1944: 206) in the usage of the term paravomerine for the patches of teeth appearing on two thin bony plates ventral to the parasphenoid bone.

of the Plethodontidae. The adult structures are basically similar, except for a few details of size and shape.

### MYOLOGICAL CONSIDERATIONS

Most striking muscular differences in salamanders are found in the musculature of the neck and the throat. This general region exhibits changes in both the superficial and the deep muscles of the various genera which are usually associated with the adaptations of the hyoid apparatus. *Desmognathus* and *Leurognathus* are no exceptions; in fact some of the most pertinent differentiations between the Desmognathidae and other families are found in the character and extent of development of this musculature.

There are two pairs of muscles in *Desmognathus* and *Leurognathus* that are extraordinarily developed when compared to analogous muscles in other salamanders. On the dorsal side of the animals we find the curious *M. temporalis* which has its origin on the posterodorsal margin of the atlas and whose fibers encircle a strong tendon that passes forward over the surface of the cranium, turns ventrad on the posterior edge of the orbit of the eye and is inserted on the tip of the coronoid process of the mandible. This tendon immobilizes the muscle and consequently the mandible, as Dunn (1926: 59) has indicated. To open their mouths desmognathids have to raise the whole skull and this is accomplished by the powerful dorsal and lateral muscles of the neck. Here is a condition different from any other family of salamanders, one that I regard as of invaluable taxonomic importance.

On the ventral side of desmognathids we find a bilobate enlargement of the gular region by means of which members of the family can be readily recognized externally. Its prominence gives this family what Piatt (1935: 222) has called "the characteristic *Desmognathus* profile." This enlargement so noticeable externally, is caused by the tremendous development of the gularis muscle<sup>‡</sup> in those forms. Upon removal of the skin these muscles stand out very prominently (see Pl. XI, fig. A). They originate on the quadrate, the articular, and the dorsolateral fascia; their insertion is on the skin of the gular fold and the pectoral fascia.

An interesting condition in the myology of salamanders is the direct correlation between the extent of attachment of the tongue and the posterior reach of the *M. subarcualis rectus*, the muscular cup

<sup>‡</sup> Piatt (1935: 222) and (1940: 10) has shown that this structure is really made up of two separate muscles, a large quadrato-pectoralis and a small, delicate gularis. However, Eaton (1937: 324) pointed out the convenience of using the name gularis to denominate the entire structure for purposes of simplicity.

that encloses the ceratobranchial cartilage and which is primarily used in extending the tongue (Francis, 1934: 61). All desmognathids have an attached tongue, while the Plethodontidae, with its great variety of genera, has forms in which the tongue has become freed from the floor of the mouth and capable of considerable protrusion. Those plethodontid forms with attached tongues may be regarded as more primitive. Plethodontid salamanders of the genera *Eurycea* and *Pseudotriton*, with a tongue free all around, have a long, far reaching subarcualis rectus, while the genera of Desmognathidae, together with those genera of plethodonts that have the tongue attached in front, have a shorter, subarcualis rectus. It seems that the tongue attachment tends to hinder the development of the subarcualis rectus, as the maximum extension of the tongue is definitely limited to a fixed measurement by this attachment. However, in those forms where there is no lingual attachment, the movement of the tongue has no other limit except that imposed by the maximum action of the subarcualis rectus itself.

Another noticeable and presumably important character is the position assumed by preserved specimens of *Desmognathus* and *Leurognathus*. Their head is bent downward giving a pronounced *rigor mortis* appearance on the anterior part of the body with the nape raised as the apex of an inverted letter V. This would suggest some unknown inherent quality of the musculature which is not present in the Plethodontidae. I have not been able to observe this peculiar condition in any other forms.

#### CIRCULATORY AND RESPIRATORY SYSTEMS

I have made no original study of the circulatory and respiratory systems of the Desmognathidae. However, I have examined such papers as would seem pertinent in this field. Among these the most important is the article by Seelye in 1906. Here a study was undertaken of the similarities and differences between a representative member of the family Desmognathidae, *Desmognathus fuscus*, and a member of the family Plethodontidae, *Spelerpes fuscus* [= *Hydromantes genii italicus*]. This work was in turn partially based on the work done on *Hydromantes* by Bethge in 1898. No differences were found in the respiratory system, yet a résumé was made of the differences in the circulatory system which I quote as follows:

"1. The vena subclavia entering the sinus venosus directly, instead of first opening into the ductus Cuvieri; and the right and left venae subclaviae opening together into the sinus on its left side.

"2. The vena abdominalis arising, not from the venae iliacae, but from the venae iliacae communes.

"3. A side tributary of the vena lingualis, observed, however, only on the left side.

"4. The arteria cutanea, a branch of the arteria pulmonalis, instead of a branch of the arteria subclavia.

"5. Four arteriae gastricae at anterior end of stomach, instead of two; three of these go to one side (the left).

"6. The presence of the arteria epigastrica, an important branch from the aorta just anterior to the arteria iliaca."

After considering these facts one is led to the conclusion that these differences are of taxonomic importance. It is not only one single detail, but an accumulation of differences between *Desmognathus* and *Hydromantes* in the morphological structures of one single system which seem to indicate no less than distinction on the family level.

#### REPRODUCTIVE SYSTEM

The testes and vasa deferentia of all members of the family Desmognathidae are covered by a deeply pigmented mesentery of coal black color. Since the first part of the century many biologists have tried to associate testicular pigmentation with external stimuli. Considerable evidence has been accumulated on the effects of light and temperature upon this pigment, but most of it is conflicting. Only of late, Finkel in 1945, has finally and definitely linked testicular pigmentation with sex hormones in opossums and ground squirrels. This work does not eliminate the strong possibility of establishing a correlation with external stimuli, but on the contrary it has indicated the necessity for such further investigations.

A few members of the genus *Plethodon* of the family Plethodontidae likewise have developed pigmented genitalia. However, I believe this case is not an illustration of relation, but one of parallel development.

#### NERVOUS SYSTEM

In the literature of the nervous system of salamanders, Murray (1897) has made a comparison between the ramifications of the spinal chord and nerves of the three forms: *Desmognathus fuscus*, *Plethodon erythronotus* [= *P. dorsalis*], and *Spelerpes fuscus* [= *Hydromantes genei italicus*]. He has noted a characteristic which I believe adds weight to the differentiation of the families Desmognathidae and Plethodontidae. He found that in the three forms the spinal nerves pierce the neural arch, however in *Plethodon*



the dorsal and ventral roots of the spinal nerve are separated by a ridge of bone on the inner surface of the neural arch. The foramen of exit, however, is single. A different condition from this last one obtains in *Desmognathus* where the dorsal and ventral roots of the spinal nerves leave the osseous canal by separate foramina.

### GLANDS

Another characteristic of the soft anatomy of the Desmognathidae which undoubtedly has bearing on taxonomic differentiation between these forms and plethodonts, is that which Mrs. Wilder (1913: 315) has noted when she studied the development of the naso-optical region in *Desmognathus*. I quote: "In connection with the development of the orbital glands it should here be noted that unlike all Urodeles (so far as the facts have been reported), *Desmognathus* has no nasolacrimal ducts. As these are present in so closely related and associated forms as *Spelerpes* and *Plethodon*, as well as in the less closely related lunged forms, their absence here has some significance which demands further study of the comparative morphology and the habits of these species."

The members of the Desmognathidae develop a submental gland in the male as a secondary sexual characteristic. Dunn (1926) and Noble (1927) have already discussed these glands. Their function seems to be hedonic. In the Desmognathidae these glands are restricted to the very anterior tip of the chin, immediately ventral to the mandibular symphysis. In this family they are composed of five or six separate fingerlike glandules arranged in a typical shape. There are submental glands in the Plethodontidae; however, their characteristics are very different from the analogous structures in the Desmognathidae. In the genera of plethodonts that I have examined the glands are flat, circular clusters of globules attached to the inner side of the skin just ventral to the floor of the mouth.

There are three sets of glands located along the walls of the cloaca of male salamanders. These glands have been found by Noble and Pope (1929) to have reproductive and hedonic functions. The anterior pair are the pelvic glands whose secretion mixes with the spermatozoa to form the head of the spermatophores. The papillae of the cloacal glands form the greater part of the villous pad on either side of the cloaca. The abdominal glands simulate a pair of wings on the posterior angle of the cloaca. In the Desmognathidae the abdominal glands have a peculiarly hard texture when compared to the same glands of other families and to the softer and fluffier pelvic and cloacal glands of the same forms. In many speci-

mens I have observed a peculiar coloration of these abdominal glands that varies from light pink to light brown. I have not found this coloration in any species belonging to other genera.

### CHARACTERS OF THE FAMILY DESMOGNATHIDAE

Future work on this problem, if directed to the soft anatomy, and especially the microscopic anatomy of the Desmognathidae will doubtless yield added evidence for the differentiation of the Desmognathidae from the Plethodontidae. Points of resemblance between the two families suggest common ancestry, or parallel development. The facts evinced from this re-examination of the problem more than suffice to confirm the separation into the two distinct families. In summation, the following combination of characters may be regarded as defining the family Desmognathidae:

1. True opisthocoelous vertebrae.
2. Hemicoelous centra.
3. A nasolabial groove present.
4. Lungs absent.
5. Tongue adherent in front and by the middle.
6. Larvae with four epibranchials.
7. Highly modified atlas.
8. Carpus and tarsus not ossified.
9. Strong tendon present in M. temporalis which immobilizes the mandible.
10. Highly developed gularis muscles.

### GENERA OF DESMOGNATHIDAE

The family Desmognathidae, as known today, comprises the two genera *Desmognathus* and *Leurognathus*. They are almost identical when observed externally. The main external difference between them is the presence of a groove from the eye to the angle of the jaw in *Desmognathus* and its absence in *Leurognathus*. This near identity has resulted in confusion and *Leurognathus* has often been mistaken for *Desmognathus* by workers in the field. However, Moore (1899), Bishop (1924), and Pope (1924 and 1928) have noted the behavior peculiar to each of these genera and on this basis they are able to distinguish them. When *Leurognathus* is exposed in water by turning a stone it either lies quietly on the bottom or glides gracefully to cover under water. This response is in sharp contrast to the darting, vigorous swimming movements of *Desmognathus quadramaculatus* or *Desmognathus phoca* when disturbed.

The basic generic differences between *Desmognathus* and *Leurog-*

*nathus* are easily discerned upon examination of the skull. Neither the premaxilla nor the vomerine bones of *Leurognathus* embrace a fontanelle as in *Desmognathus*. This condition gives the anterior part of the skull of *Leurognathus* a completely roofed appearance. The choanae of *Leurognathus* are small foramina hidden in a fold at the sides of the roof of the mouth. In *Desmognathus*, however, these are conspicuous, plainly observable openings. The ratio of the length of the orbit to the total length of the skull is higher in *Leurognathus* than in *Desmognathus*. Nevertheless after these generic differences are noticed we find that endless stream of similarities which classify these two forms as two closely related genera within the family Desmognathidae.

The loss of the type of the mysterious *Haptoglossa pressicauda* Cope allows us only to speculate as to the kinship of this form. This species was placed by Cope in the subfamily Thoriinae under the family Desmognathidae. From the description given by Cope (1893: 334) this genus could belong to the family Desmognathidae as we see it today. However, we shall never determine its exact taxonomic position until the species is again found. Dunn (1926: 429) doubtfully synonymizes this form with *Oedipus uniformis* [= *Oedipina uniformis*], yet I fail to understand how he can reconcile the adherent tongue, the compressed tail, and the relative sizes of the head, body, and tail as described by Cope with those of *Oedipina uniformis* that has totally different characters. This form could also be a plethodont, as none of its characters is conflicting with the wide variety found in this family. The family association will depend upon ascertaining the character of the vertebral structure and articulation, and other family characteristics.

As previously stated *Thorius* Cope and *Typhlotriton* Stejneger were at one time included in the family Desmognathidae. *Thorius*, however, may be promptly eliminated from it on the basis of its pseudocoelous centra, dorsal skull characters, the orbitolabial groove, the normal atlas, its free tongue, and the absence of highly developed gular muscles. I have not examined adult specimens of *Typhlotriton*, but from Moore (1900: 620) I infer that it has pseudocoelous vertebrae. This last genus may be also eliminated from the family Desmognathidae on the strength of its normal atlas and the presence of a prefrontal bone. Dunn (1926: 251) has conclusively associated this genus with the plethodontid group close to *Eurycea*, and proved its lack of relationship with the family Desmognathidae.

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## EXPLANATION OF PLATE X

FIG. A. *Thorius narisovalis*, No. 25216 EHT-HMS.

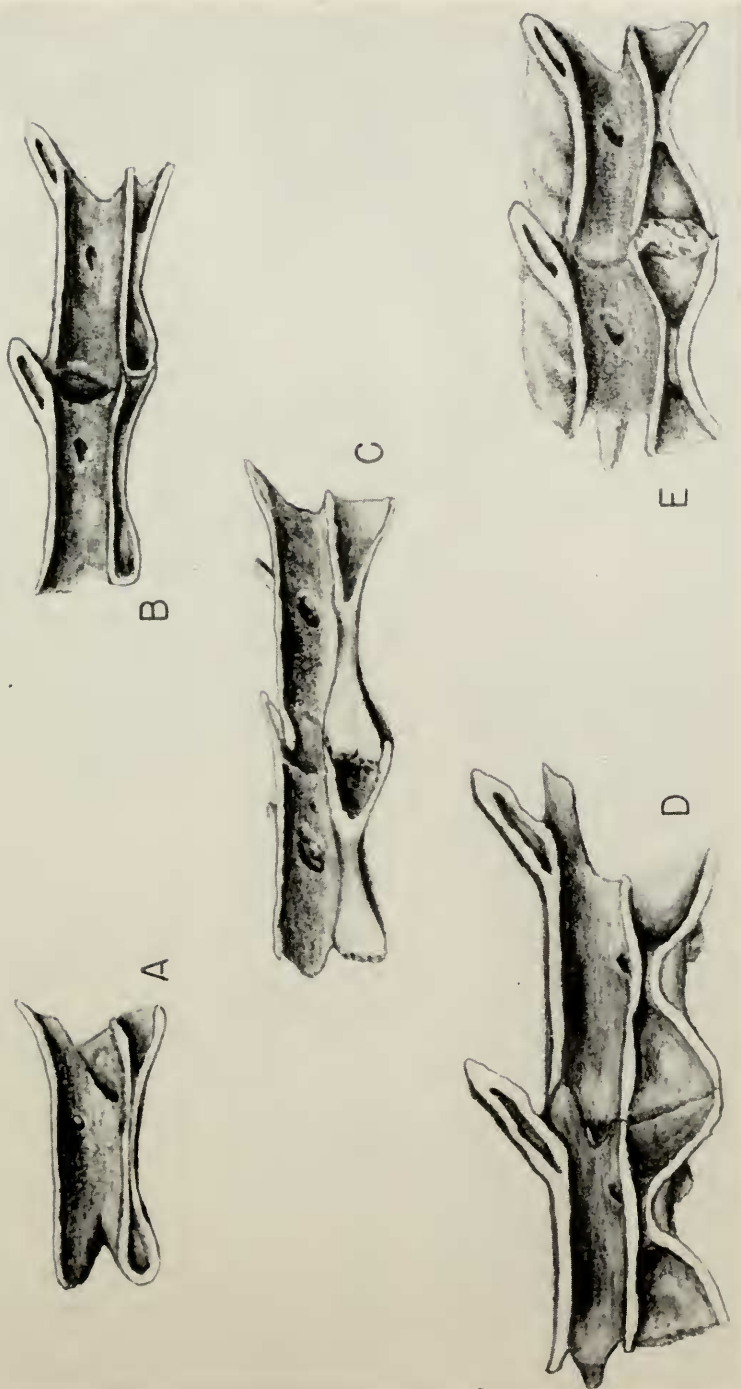
FIG. B. *Taricha torosa*, No. 18263 M. V. Z. K. U.

FIG. C. *Desmognathus fuscus fuscus*, No. 28293 EHT-HMS.

FIG. D. *Pseudotriton ruber ruber*, No. 19450 M. V. Z. K. U. (specimen 135 mm. in length).

FIG. E. *Gyrinophilus porphyriticus porphyriticus*, No. 28272 EMT-HMS (specimen 140 mm. in length).

PLATE X



Sagittal sections of presacral vertebrae (enlarged)

## PLATE XI

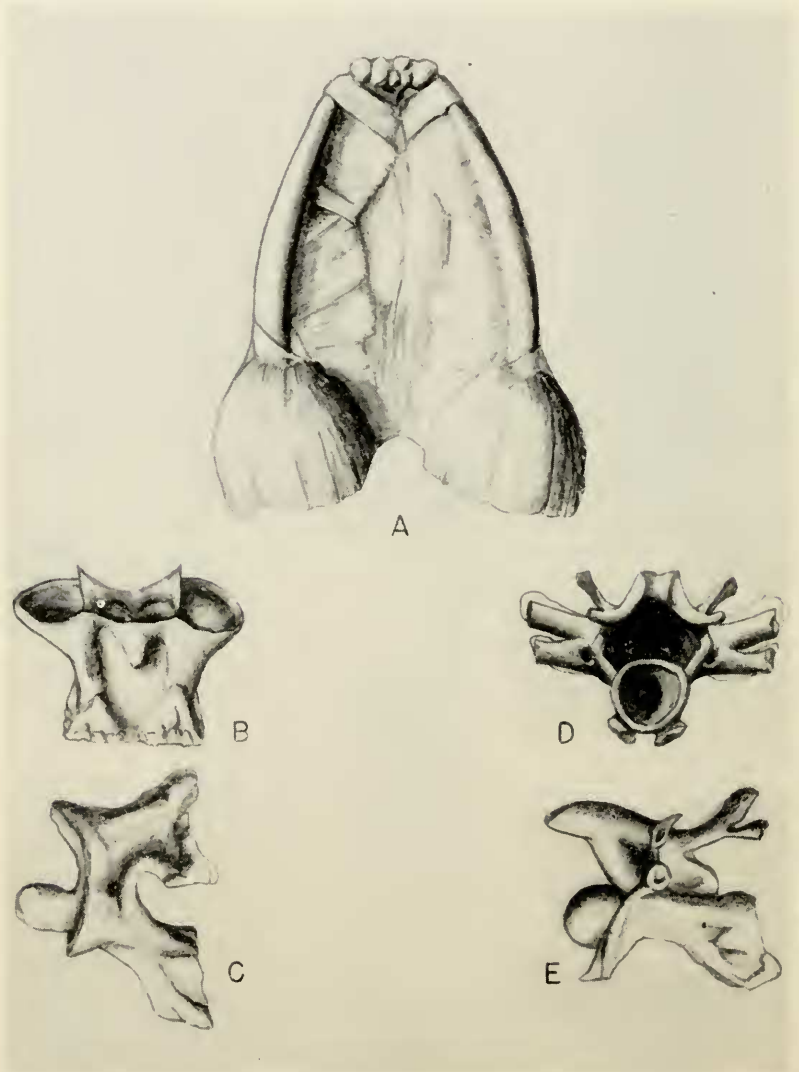


FIG. A. Ventral view of the throat musculature of an adult male of *Desmognathus ochrophacus ochrophacus*, showing the development of the gularis muscles and the submental gland.

FIG. B. Dorsal view of the atlas of *Desmognathus fuscus fuscus* showing the reduction of the odontoid process.

FIG. C. Side view of the atlas of *D. fuscus fuscus* showing the transverse ridge for the attachment of the temporal tendon.

FIG. D. Posterior end view of anterior presacral vertebra of *D. fuscus fuscus* showing the processes arising from the postzygaphophysis.

FIG. E. Side view of D.